

FIRST INSTAR DESCRIPTION OF *KORSCHTELLELLUS GRACILIS* (GROTE) AND *STHENOPIS AURATUS* (GROTE) (LEPIDOPTERA: HEPIALIDAE) WITH A CONSIDERATION OF CLADISTIC RELATIONSHIPS BETWEEN SETAE

JONATHAN G. LEONARD, JOHN R. GREHAN, AND BRUCE L. PARKER

Entomology Research Laboratory, University of Vermont,
655-B Spear Street, South Burlington, Vermont 05403

Abstract.—The external morphology and chaetotaxy of first instar *Korscheltellus gracilis* (Grote) and *Sthenopis auratus* (Grote) are described. The larvae of *K. gracilis* are smaller and have fewer microtrichia than *S. auratus*. The only difference in chaetotaxy involves the absence of pore Va from the head of *S. auratus*. The setal nomenclatures of Hasenfuss (1969) and Wagner (1987) are evaluated and used for description. The classifications of Hinton (1946) and Hasenfuss (1969) are compared for the homology of cranial setal groups. In a comparison of the P and V setae we suggest that homologies are treated as apomorphies by Hasenfuss, while Hinton's setal homologies represent plesiomorphies. Hasenfuss's (1969) nomenclature renders the cranial chaetotaxy of Hepialidae identical to the Ditrysia. We suggest that the prothoracic association of SD1, SD2 and D2 may represent an exoporian apomorphy. Cladistic criteria provide a useful technique for resolving homology problems and choosing between alternative systems of chaetotaxy.

Korscheltellus gracilis (Grote) is a common eastern North American insect of upper elevation boreal forest soils (Wagner, 1988; Tobi et al., 1989; Wagner et al., 1989; Leonard et al., 1991; Wagner et al., 1991; Grehan et al., 1992; Tobi et al., 1992). Larvae feed on mosses, ferns and tree roots, including roots of red spruce (*Picea rubens* Sargent) and balsam fir (*Abies balsamea* (L.) Miller), which are species of major concern for environmental scientists interested in boreal forest dynamics and tree decline (e.g., Reiners and Lang, 1979; Siccama et al., 1982; Hornbeck and Smith, 1985; Hain, 1987; Klein and Perkins, 1988; Vogelmann et al., 1988; Bonan and Shugart, 1989; Pitelka and Raynal, 1989; Silver et al., 1991; Smith, 1991).

Larvae of *Sthenopis auratus* (Grote) feed on roots, stems and leaf bases of ostrich fern (*Matteuccia struthiopteris* (L.) Todaro) (McCabe and Wagner, 1989) and wood fern (*Dryopteris campyloptera* Clarkson) (JGL unpubl. data). They are infrequently recorded from the spruce-fir zone (1,000 m elev.) on Camels Hump Mt., Huntington, VT, but are common at 200 m in the University of Vermont Experimental Research Forest, Jericho, VT. At our Camels Hump field site one *S. auratus* and 1,200 *K. gracilis* larvae were recovered from 110 soil pits (Leonard et al., 1991).

The post-first instar chaetotaxy of *K. gracilis* was described by Wagner et al. (1989) using Stehr's (1987) modification of Hinton (1946). The post-first instar of *S. auratus* was described and the chaetotaxy discussed, but not illustrated, by McCabe and Wagner (1989). Hepialid larvae have been described by a number of authors (e.g., Dyar, 1895; Packard, 1895; Fracker, 1915; Forbes, 1923; Gerasimov, 1937, 1952; Hinton, 1946; Hasenfuss, 1963, 1969; Aitkenhead and Baker, 1964; Hardy, 1973;

Table 1. Hepialidae head chaetotaxy according to Hinton (1946), Hasenfuss (1963, 1969), Wagner (1987), and Wagner et al. (1989) (modified from Stehr, 1987). Setal names in parentheses, mislabeling in square brackets.

Hinton	Hasenfuss	Wagner
A1 (Anterior)	A3	A1
A2	A2	A2
A3	P2	A3
O1 (Ocellar)	A1	S1 (Stemmatal)
O2	O1	S2
SO1 (Subocellar)	SO1	SS1 (Sub-stemmatal)
SO2	SO2	SS2
SO3	SO3	SS3
F1 (Frontal)	F1	F1
Fa (pore)	Fa	Fa
C1 (Clypeal)	C1	C2
C2	C2	C1
L1 (Lateral)	L1	L1
La (pore)	La	La
P1 (Posterodorsal)	P1	P1
P2	V1 (Vertexal)	P2
V2	V2	MD2 [MD1]
V3	V3	MD3
Va (pore)	Va	MDa [MD2]
G1 (Genal)	G1	MG1 (Micro-genal)
G2	O3	MG2

Grehan, 1981; Grehan et al., 1983; Yasuda and Abe, 1986; Wagner, 1987; McCabe and Wagner, 1989; Nielsen and Kristensen, 1989; Wagner et al., 1989; Common, 1990; Boudinot, 1991). Nomenclatural systems for hepialid chaetotaxy and cranial pores proposed as modifications to Hinton (1946) include Hasenfuss (1969), Nielsen and Kristensen (1989), Yasuda and Abe (1986), Stehr (1987), and Wagner (1987). With the exception of Hasenfuss (1963, 1969), the alternatives are presented without extensive comparative corroboration.

The chaetotaxy of first instars is different from second and later instars and may be more conservative. First instars, therefore may contribute significant information about phylogenetic relationships within the Exoporia (Nielsen, 1989). However, out of an estimated 500 species in the Hepialidae (Kristensen, 1978), descriptions of first instar Hepialidae are limited to about 10 species (Dyar, 1895; Fracker, 1915; Hinton, 1946; Aitkenhead and Baker, 1964; Grehan, 1981; Grehan et al., 1983).

This description of *K. gracilis* and *S. auratus* first instars will refer to Hasenfuss's (1969) setal nomenclature for the head, Wagner's (1987) system for the prothorax (TI) (with the addition of the Hasenfuss [1963] notation for the **XD** pores which were not illustrated in Wagner [1987]), and Hinton (1946) for the meso- and metathorax (TII, TIII) and abdomen (A1–A10). We will discuss these nomenclatural systems in relation to our observations on the first instars and comparisons with Hepialidae described in the literature. Tables 1 and 2 compare the hepialid nomenclatural systems currently in use.

Table 2. Prothorax chaetotaxy used for Hepialidae according to Hinton (1946), Nielsen and Kristensen (1989), Wagner (1987), and Wagner et al. (1989).

Hinton	Nielsen and Kristensen	Wagner
D1 (Dorsal)	D1	D1
D2	D2	SD2 (Sub-dorsal)
XD1 (Extra-dorsal)	XD1	XD1
XD2	XD2	XD2
XDb (pore)	XDa	—
XDa	XDb	—
XDc	XDc	—
SD1	SD1	SD1
SD2	SD2	D2
L1 (Lateral)	L1	L1
L2	L2	L2
L3	L3	L3
SV1 (Sub-ventral)	SV1	SV1
SV2	SV2	SV2
MV2 (Mid-ventral)	MV2	MV2
MV3	MV3	MV3
V1 (Ventral)	V1	V1

We have confined our description to body setae and pores with the exclusion of the larval thoracic leg and abdominal proleg setae. Comparative chaetotaxy of thoracic and abdominal legs has received little attention but several alternative systems have been proposed (e.g., Gerasimov, 1952; Birket-Smith, 1984; Nielsen and Kristensen, 1989).

MATERIALS AND METHODS

Korscheltellus gracilis eggs were collected on 25 July 1990 from a female that was in copula on a balsam fir branch apex 1 m above ground at 1,000 m elevation on Camels Hump Mountain, Huntington, Vermont. The mating pair and fir branch were enclosed in a plastic bag after the evening flight (approximately 9 pm EST) and eggs recovered the following morning. *Sthenopis auratus* eggs were collected on 14 July 1990 from a female found in copula on the frond tip of ostrich fern at the University of Vermont Experimental Research Forest in Jericho, VT. Eggs were incubated on moist filter paper inside petri dishes in a saturated atmosphere at 18°C.

First instars were preserved in 70% EtOH. The head capsules of 8 *S. auratus* and 24 *K. gracilis* were measured to the nearest 0.001 mm. Means and 95% confidence intervals for head capsule measurements were computed using univariate descriptive procedures in SAS (1985). Sub-samples of larvae were randomly chosen for examination by scanning electron (SEM) and light microscopes. Light microscope slides were prepared as described in Aitkenhead and Baker (1964). In addition, some larvae were cleared with KOH and temporarily slide-mounted in glycerine. Descriptions presented refer to both species unless otherwise indicated.

RESULTS

Eggs of *K. gracilis* hatched in 26 days and those of *S. auratus* hatched in 30 days. Eggs of *S. auratus* were larger than those of *K. gracilis*.

Head. The head capsule is straw-colored and large relative to the body size, especially for *K. gracilis*. The head capsule widths of *S. auratus* (mean = 0.546 mm, standard error \pm 0.002 mm, N = 8) were significantly larger than that of *K. gracilis* (0.332 mm \pm 0.002 mm, N = 24). Head setae of *S. auratus* were shorter relative to the head size than on *K. gracilis* and the shape of the head capsule, adfrontal suture, and mandible was different between species (Figs. 1–6).

The antenna appears 3-segmented, but may be 2-segmented as described for *Fraus* by Nielsen and Kristensen (1989). Antenna is shorter and thicker than in the post-first instar (cf. McCabe and Wagner, 1989; Wagner et al., 1989). Each antenna bears three conical sensilla and three trichoid sensilla with the lateral trichoid sensillum 1.5 times the length of the antenna. The anterior-most trichoid sensillum arises from the base of the most anterior conical sensillum (Figs. 7–8).

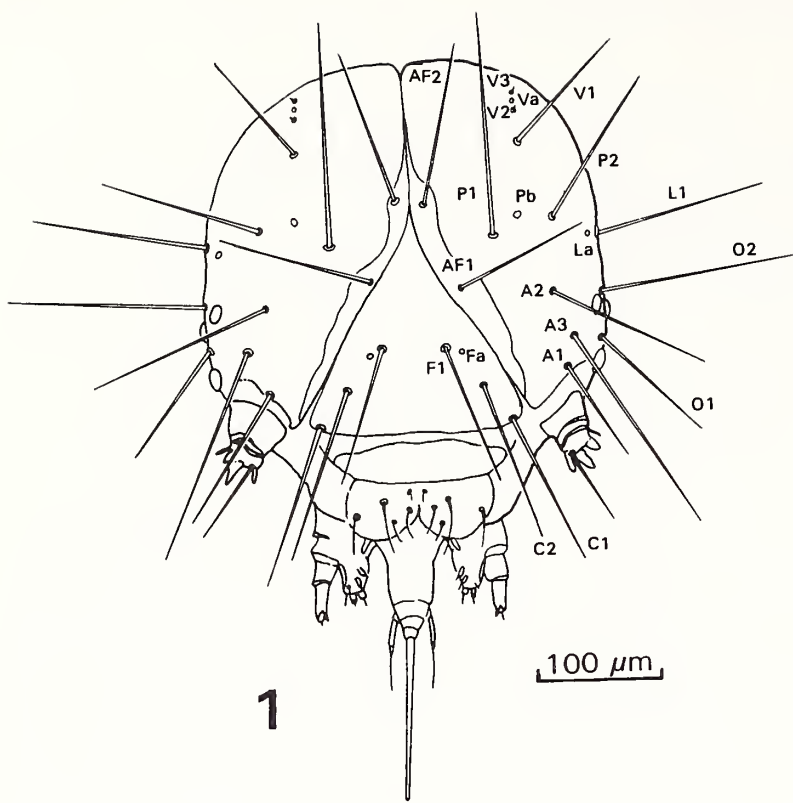
The labrum is deeply cleft with 5 pairs of setae. The mandible has 5 teeth. The middle three teeth are serrate on ventrad edge. The mandible has 2 setae; one small seta located on the dorsal tooth, the second 1.5 times the mandible length and inserted into the mandible base (Figs. 3, 6).

The maxillae of both species are as described for post-first instar *K. gracilis* (Wagner et al., 1989), except the palpi are thinner and more elongate (Figs. 9–13). Each maxilla bears a stout trichoid sensillum on the dististipes, a 3-segmented maxillary palpus, and a mesal lobe (lobarium) with 1 trichoid sensillum on the base and 7 sensilla on the apex. Unlike later instars, the basal trichoid sensillum on the mesal lobe is subequal in length to the lobe. The apical sensilla of the mesal lobe consists of 2 styloconic sensilla, 3 small trichoid sensilla, and 2 larger trichoid sensilla. The basal segment of the maxillary palpus bears a pore on the lateral side. The apical end of the palpus bears larger, more prominent sensilla than in later instars including at least 4 trichoid sensilla and 1 squamiform sensillum (Fig. 11–13). (The maxillary palpus of *K. gracilis* is incorrectly labeled the labial palpus in Wagner et al. [1989: 721, Fig. 11].)

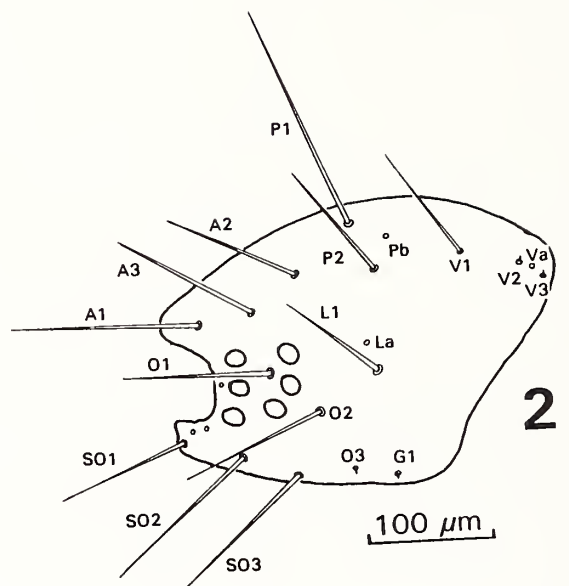
The hypopharynx and labium for both *K. gracilis* and *S. auratus* are nearly as described for post-first instars by Wagner et al. (1989). The labial palpus is 2-segmented, but the number is uncertain for the later instars (Wagner et al., 1989). The distal segment is short and conical, bearing a trichoid seta subequal in length to the palpus (Fig. 12). The spinneret of both species is approximately equal to the length of the maxillolabial-hypopharyngeal complex and is oriented ventro-caudad (Figs. 1, 4, 14–15). The hypostomal plates are not fused at the midline for both *K. gracilis* and *S. auratus* first instars.

In larvae of *K. gracilis* the pore **Va** (=MD2 of Wagner et al., 1989) is positioned between the two vertex (**V**) setae (N = 6) as in other Hepialidae (Figs. 1–2), but missing in *S. auratus* (N = 7) (Figs. 4–5, 16, 17). The pore **MDa** was misidentified as microseta **MD2** in Wagner et al. (1989), resulting in the anterior microseta **MD2** being misidentified as **MD1**. Setae **A1** and **S1** were also mislabelled (Wagner et al., 1989:721, fig. 8) as **A3** and **S3** respectively.

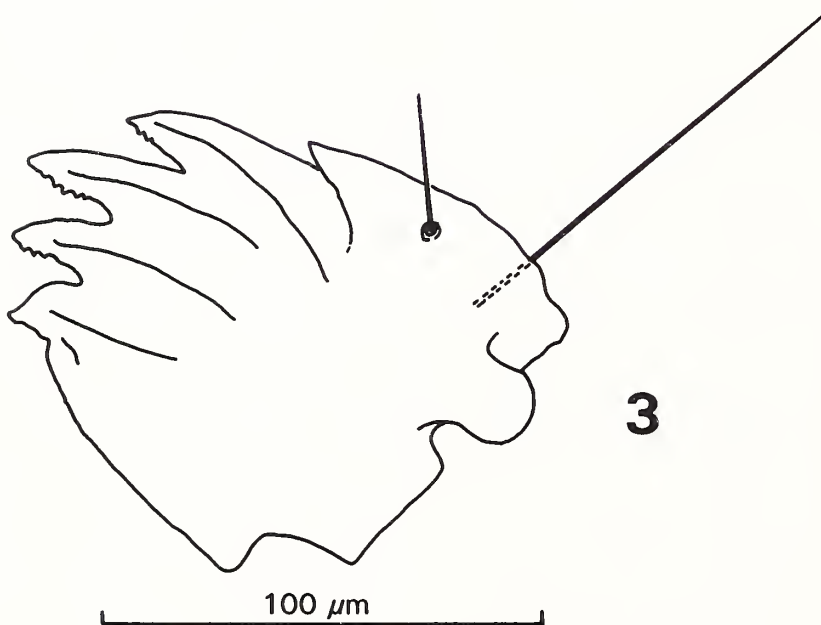
First instars of both *K. gracilis* and *S. auratus* show all of the setal characters present in later instars except for the lack of subprimary setae (see Tables 1 and 2



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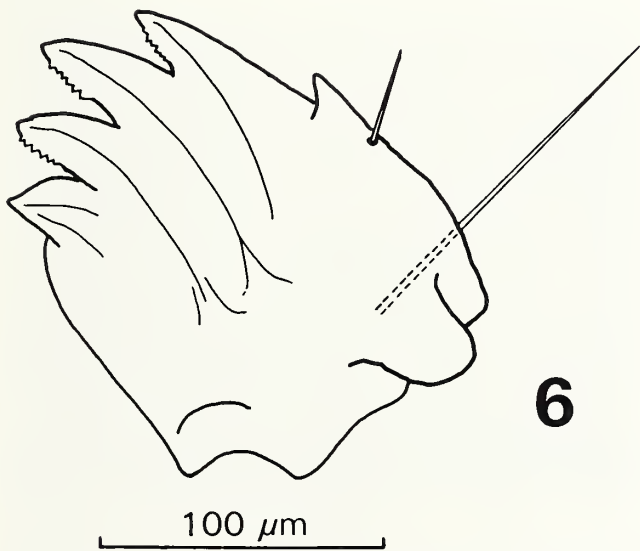
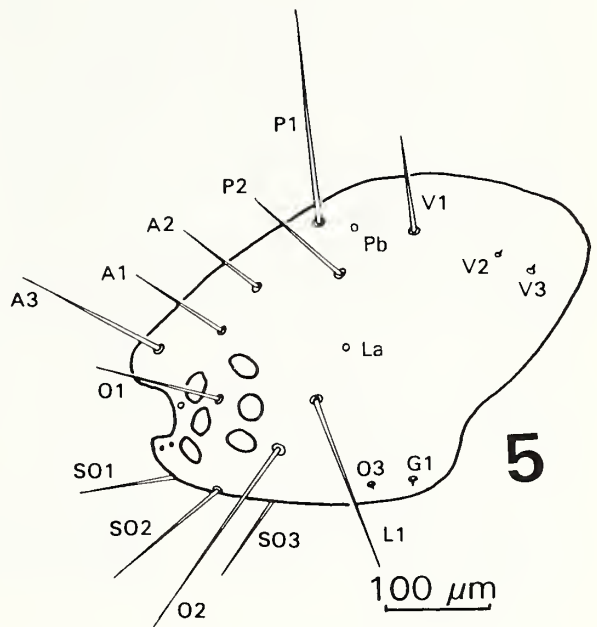
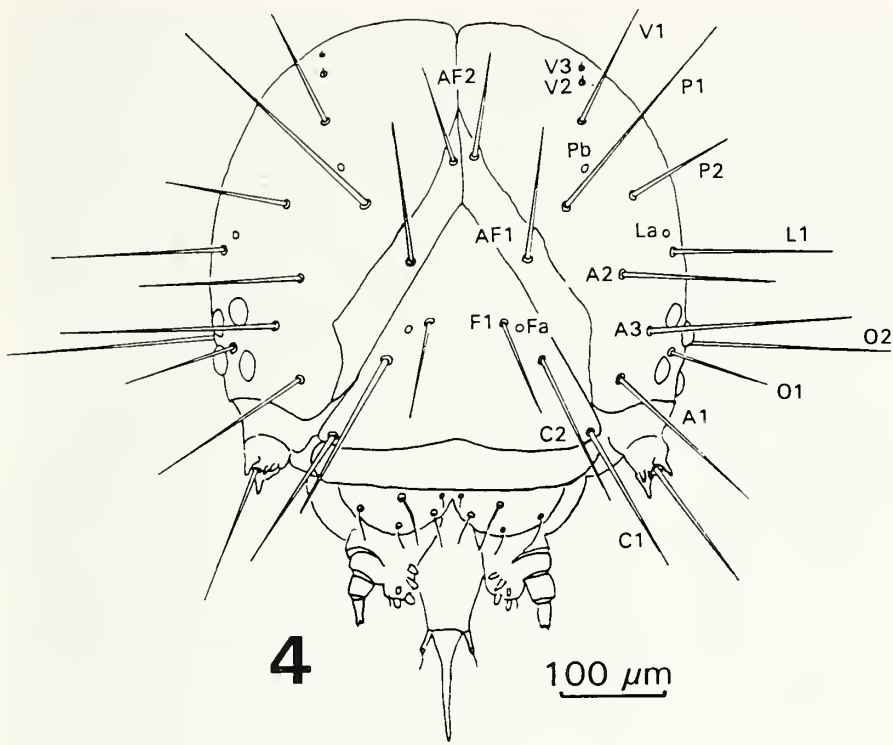


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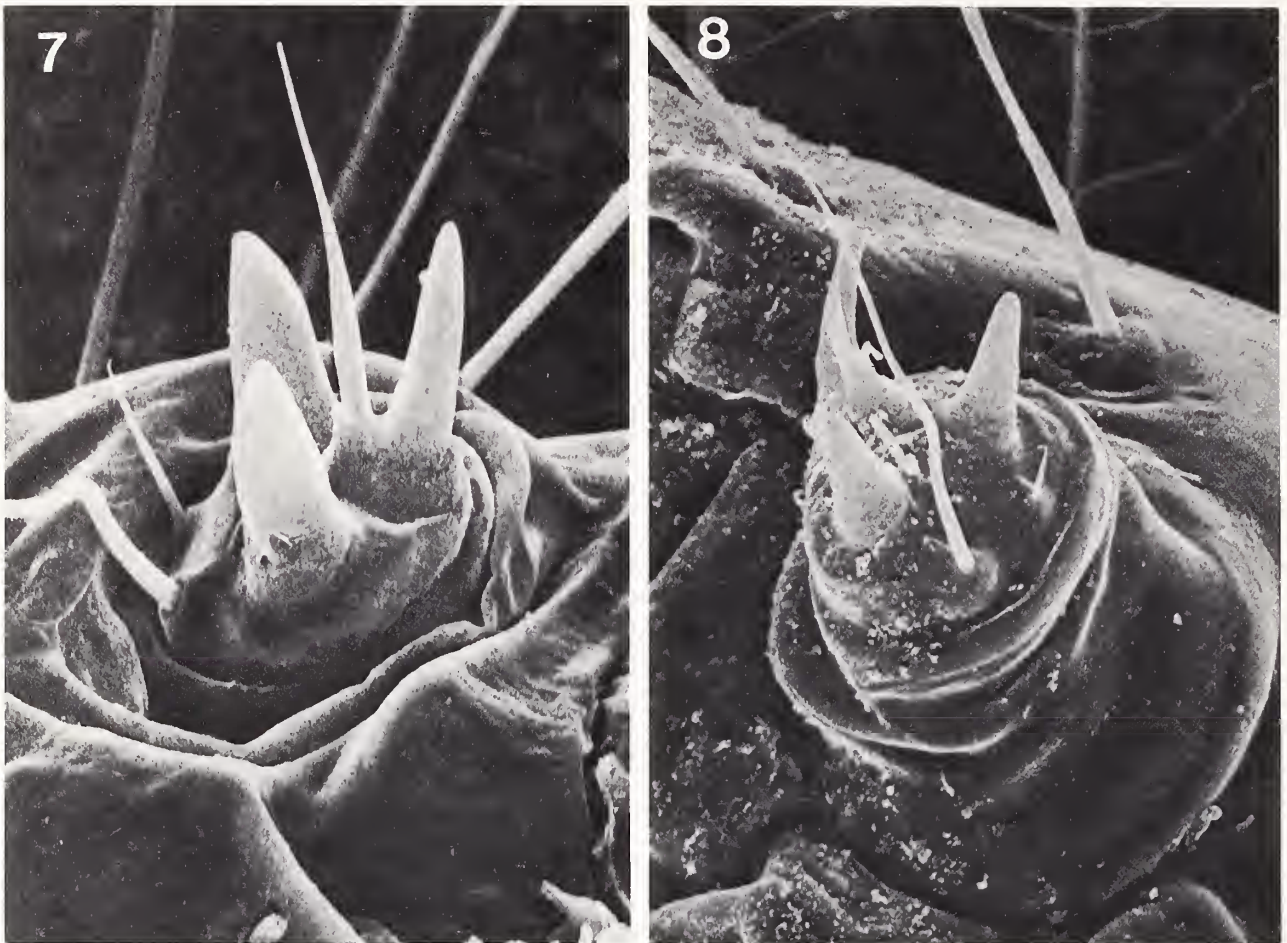


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Figs. 1-3. *Korscheltellus gracilis* first instar head chaetotaxy. 1. Dorsal view. 2. Lateral view. 3. Mandible.



Figs. 4–6. *Sthenopis auratus* first instar head chaetotaxy. 4. Dorso-frontal view. 5. Lateral view. 6. Mandible.

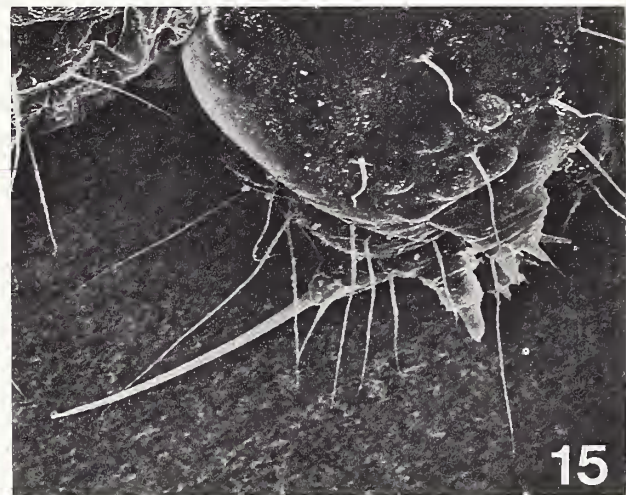
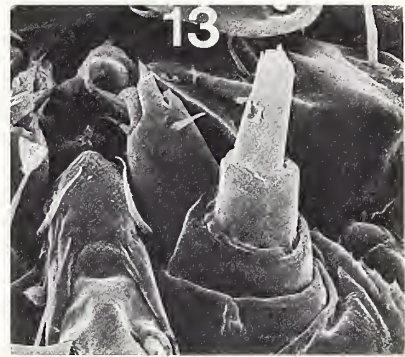
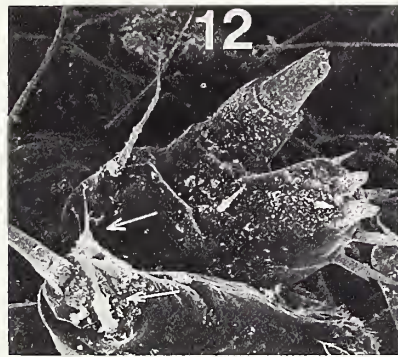
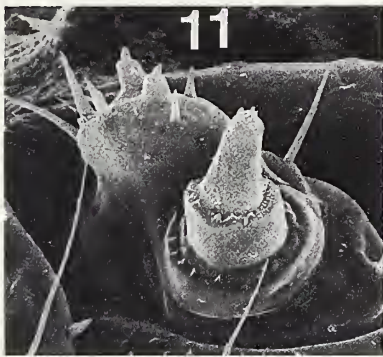


Figs. 7–8. Scanning electron micrographs. 7. Antenna of *Korscheltellus gracilis*, 1095 \times . 8. Antenna of *Sthenopsis auratus*, 535 \times .

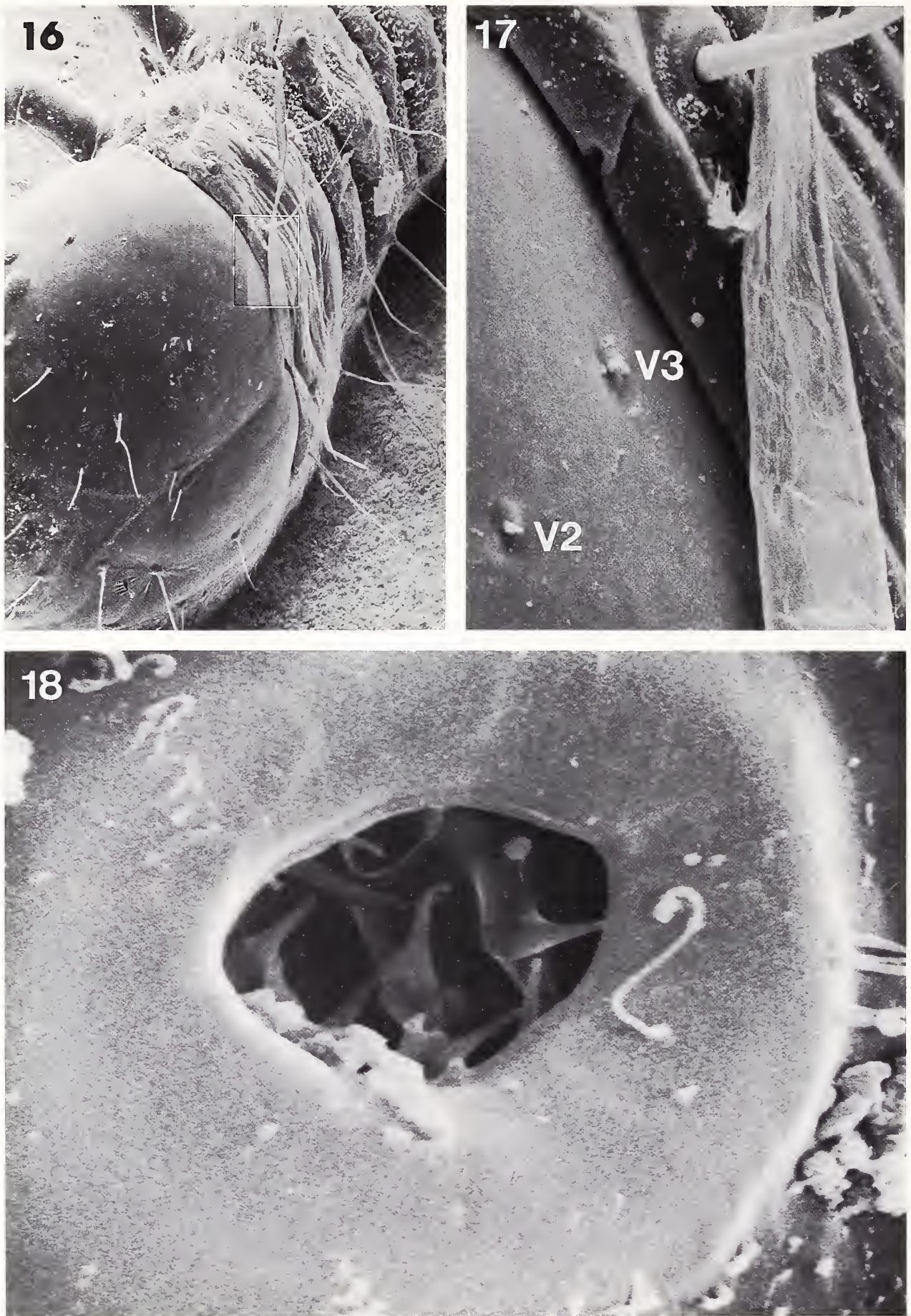
for nomenclature). First instars lack: **L2** on TII, TIII and A9; **SV2** on TII and TIII, and A7–A9; **L3** on all segments; **SV3** on A1–A9.

Thorax. Both species have microtrichia on all thoracic and abdominal segments but *S. auratus* is more densely covered. Conical microtrichia were present in the TI spiracular opening of *S. auratus* (Fig. 18) but absent in *K. gracilis*. The number and relative positioning of setae is the same as previously reported for other hepialid first instars. TI lateral setae (**L1**, **L2**) are on a laterad sclerotized plate just ventrad of the prothoracic shield (Figs. 19, 21). Setae **SD1**, **SD2**, and **D2** are on a thinly sclerotized latero-caudad extension of the prothoracic shield. In comparison to **D2**, setae **SD1** and **SD2** are thicker, longer and inserted into larger sockets (unlike post-first instars). **SD** setae are not subtended by dense microtrichia as in post-first instars. **D2** is closer to **SD** setae than to **XD** setae as in post-first instars. **MV** setae are of approximately equal length.

On TII and TIII of both species, **D1** pinacula are fused across the midline. Setae **D2**, **SD1** and **SD2** are on a single non-melanized pinaculum in *K. gracilis* on both TII and TIII (Fig. 19) unlike post-first instars where on TIII **D2** is on a separate melanized pinaculum (Wagner et al., 1989). In *S. auratus* **D2** is on a separate melanized pinaculum on TIII (Fig. 21), as in post-first instars (McCabe and Wagner, 1989). **MD1** is the same length as **MSD** setae in *K. gracilis* first instars which differs from post-first instars where **MD1** is longer. **MD1** in the first instar of *S. auratus* is slightly longer than the **MSD** setae. The thoracic leg claw basal tooth ends near one-

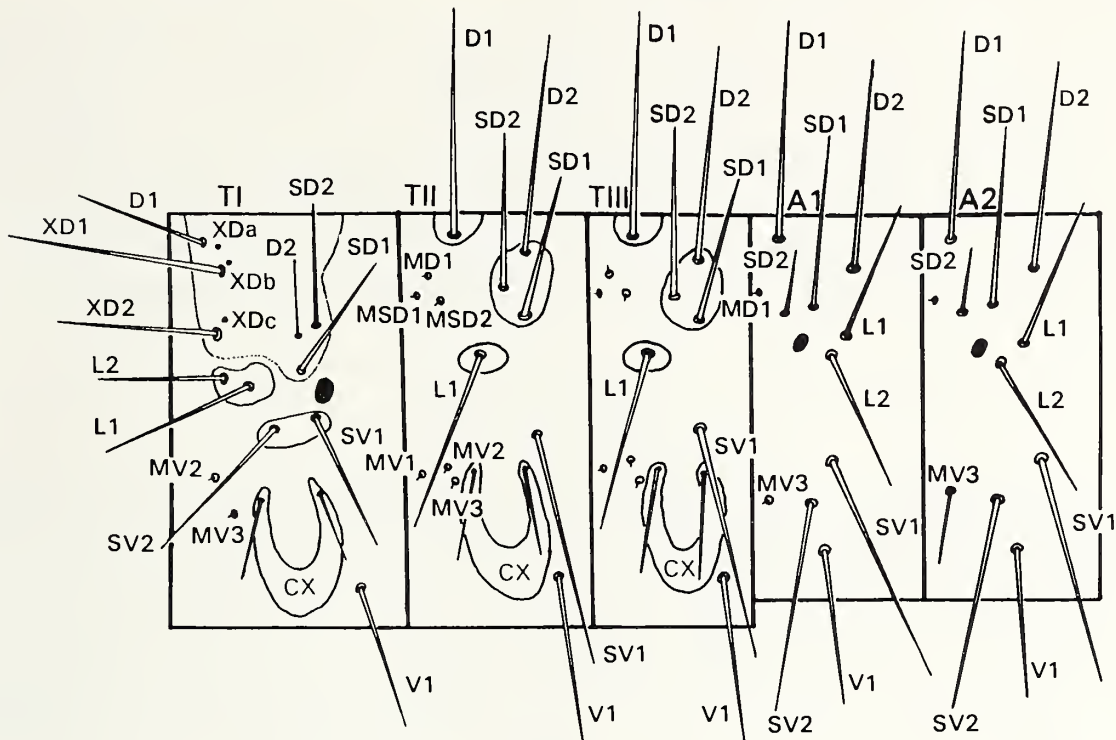


Figs. 9–15. Scanning electron micrographs. 9. Maxillolabial-hypopharyngeal complex of *Korscheltellus gracilis*, 175 \times . 10. Maxillolabial-hypopharyngeal complex of *Sthenopis auratus*, 155 \times . 11. Maxilla of *Sthenopis auratus*, 225 \times . 12. Maxillolabial detail of *Sthenopis auratus*, 225 \times . Arrows point to labial palps. 13. Maxilla of *Korscheltellus gracilis*, 465 \times . 14. Head of *Korscheltellus gracilis* in lateral view, 310 \times . 15. Head of *Sthenopis auratus* in lateral view, 125 \times .

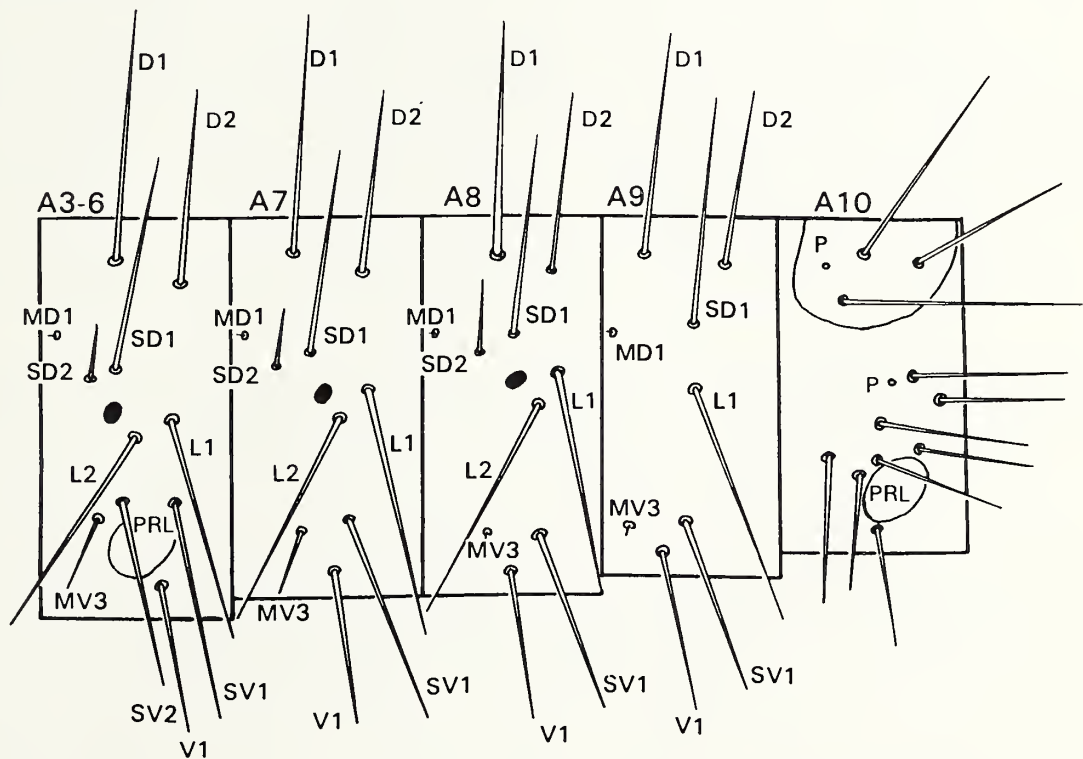


Figs. 16–18. Scanning electron micrographs. 16. Vertex setae of *Sthenopis auratus*, 145 \times . 17. Detail of box from Figure 16 showing V setae. 18. Detail of spiracle of *Sthenopis auratus* showing conical microtrichia, 640 \times .

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Figs. 19-20. Chaetotaxy of *Korscheltellus gracilis* first instar larvae; spiracle represented by shaded ellipse. 19. Thorax and first two abdominal segments; CX, coxa. 20. Abdominal segments 3-10; non-melanized pinacula bounded by solid lines; P, pore; PRL, proleg.

third of the claw length (Figs. 23–24), but in second to final instars the tooth ends near midlength (Wagner et al., 1989: fig. 12).

Abdomen. The number and relative positioning of abdominal setae is the same as for other first instar hepialids. **MV3** is a proprioceptor microseta on A1, A8, and A9, but a tactile macroseta on A2–A7 (Figs. 20, 22). In *S. auratus* a darkened melanized pinaculum encloses **SD1** and **SD2** while the **L** setae are each enclosed in a separate melanized pinaculum as in post-first instars. Crochets in both species are in biserial ellipses with a prominent inner row (Figs. 25, 26). Segment A10 has 11 setae and two pores: anal shield with 3 setae and a pore; remaining pore and 8 setae below shield.

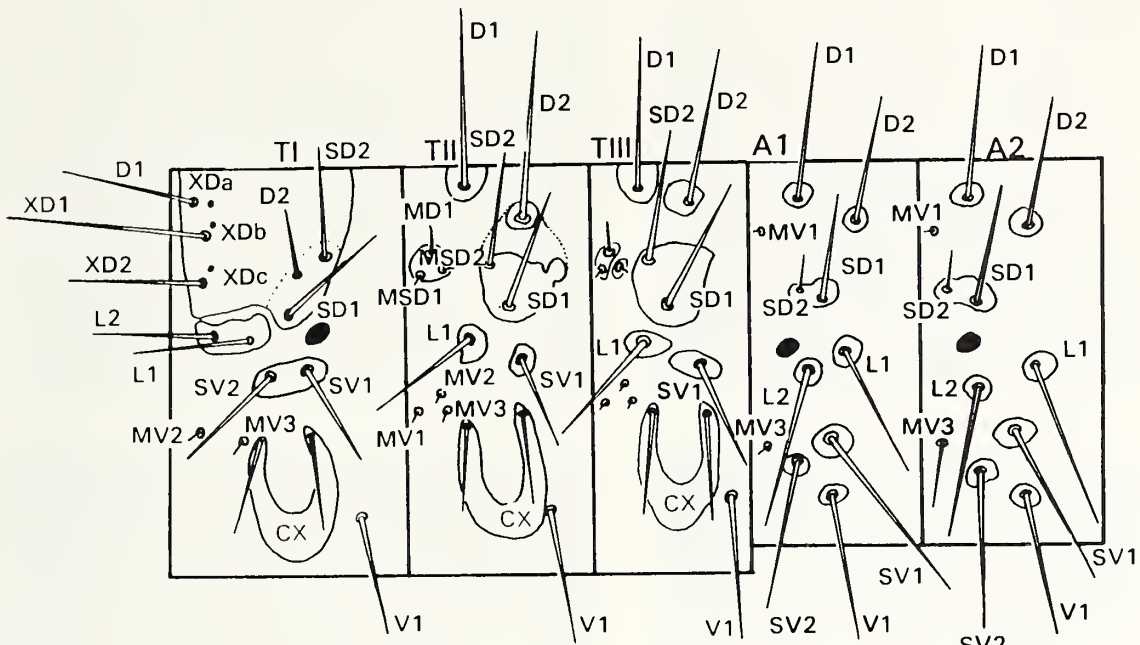
DISCUSSION

Chaetotaxy is important in the systematics of the Lepidoptera because it is used to distinguish taxa and to define monophyletic groups. At present there is a lack of explicit analytical criteria for identifying chaetotactic homologies that confer natural setal groups. Hinton's (1946) major review emphasized comparisons among the Ditrysia and some Monotrysia including the Hepialidae. Earlier systems were already in existence (e.g., Fracker, 1915) and Hinton's (1946) nomenclatural system modified earlier proposals by Heinrich (1916) and Gerasimov (1935) (Hinton, 1946:9, Table 1). Hinton's (1946) nomenclature has received wide application, but several authors have identified problems with respect to the Hepialidae and offered modifications (Hasenfuss, 1963, 1969; Wagner, 1987; Nielsen and Kristensen, 1989). The different alternatives and their justifications are discussed as follows:

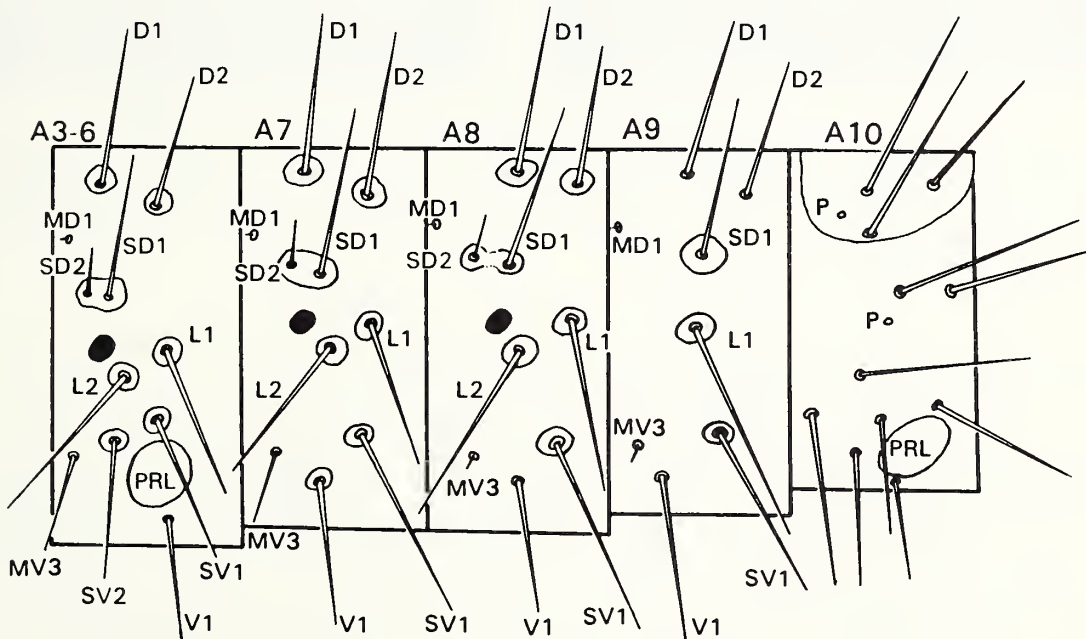
Head. Hinton's (1946) nomenclature (Fig. 27) was critically examined by Hasenfuss (1969), who was concerned with Hinton's designation of a unique genal micro seta (**G2**) and apparent absence of micro seta **V1** that renders the Hepialidae anomalous to the Ditrysia where **G2** is absent and **V1** is present. Hinton's (1946) contrast between Hepialidae and Ditrysia is based upon differences in size and position of setae (the **G** and **V** setal groups being defined by their small size as microsetae). Hinton (1946: 6) was unable to decide which of the **G** setae were represented in the Ditrysia and **V1** was presumed absent from Hepialidae because the two micro **V** setae present were necessarily identified as **V2** and **V3** by the interposition of the pore **Va** (Fig. 27).

Hasenfuss (1969) argued that setal length was a consequence of head capsule orientation and degree of retraction of the head against the thorax. He also pointed out that in leaf mining groups the longer tactile setae are present only on the leading edge and sides of the head capsule. He suggested that setal length alone does not qualify as a defining character (i.e., the equivalent of apomorphy) for inclusion of setae within particular setal groups. He noted that there are normally three vertex setae in the Ditrysia (**V1**, **V2** and **V3**) with the pore **Va** almost always between **V2** and **V3** (**Va** is sometimes offset to one side), while the genal region supports only a single seta **G1** (Fig. 28). While the homology of Ditryisian setae was stable, there were cases where the boundary between setal groups ("Musterelementgruppe") became blurred. Hasenfuss (1969) presented the *Yponomeuta* as an example with **V2** and **V3** present as microsetae while **V1** was very long and having the appearance of a macroseta. The Hepialidae show the same total number of head setae (although fewer

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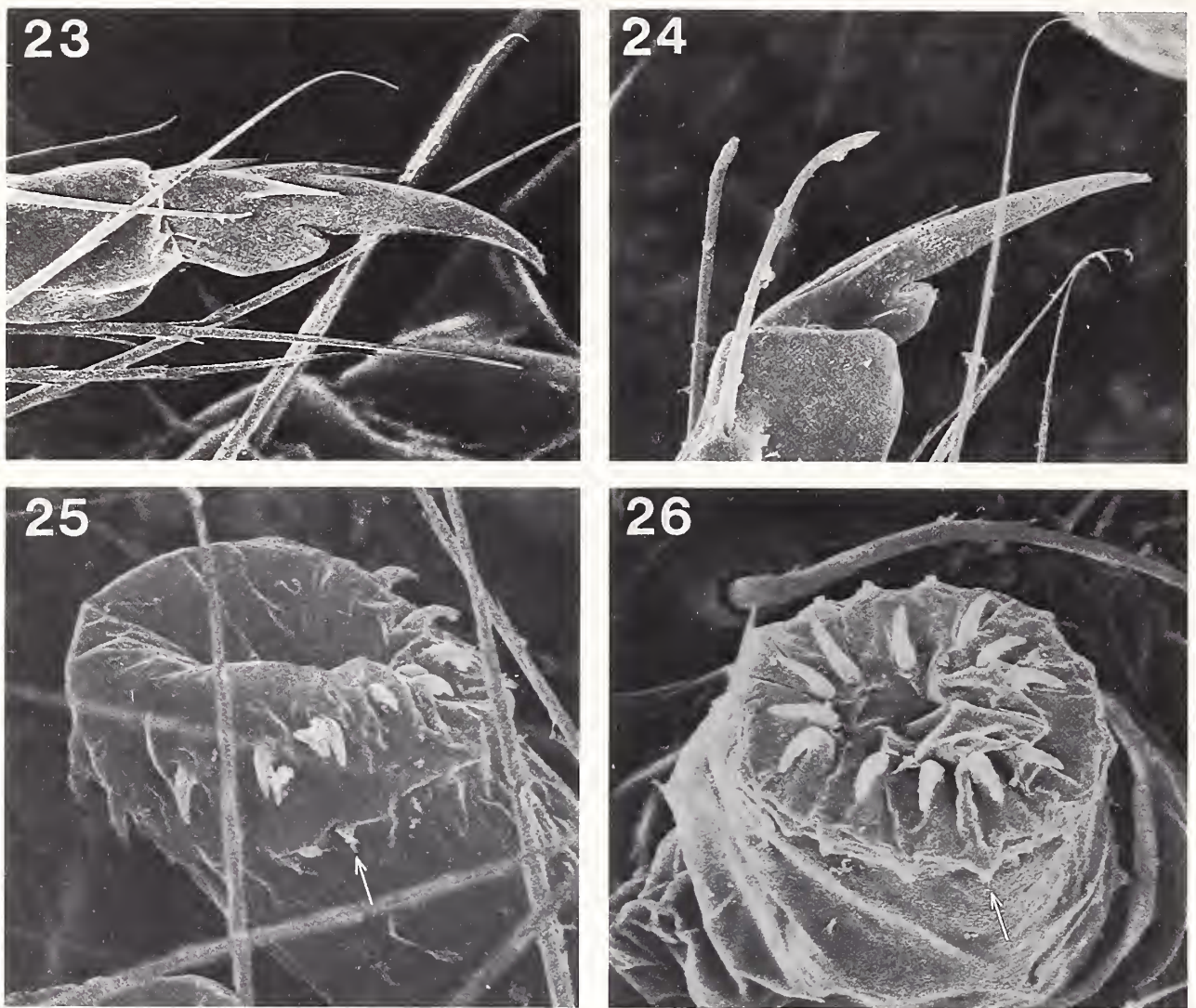


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Figs. 21–22. Chaetotaxy of *Sthenopis auratus* first instar larvae; spiracle represented by shaded ellipse. 21. Thorax and first two abdominal segments. 22. Abdominal segments 3–10; melanized pinacula bounded by solid lines; P, pore; PRL, proleg.

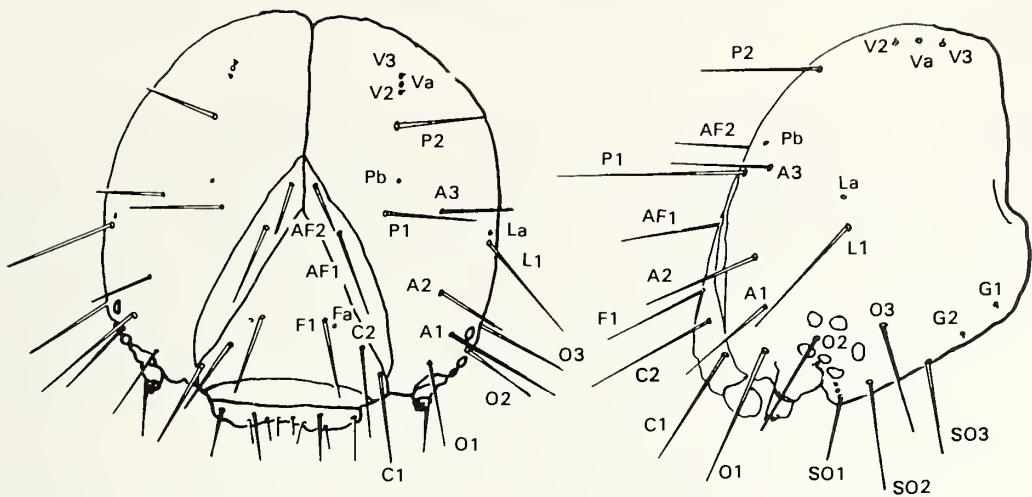
pores) as the Ditrystia, but only two microsetae occur on both the vertex (normally three in the Ditrystia), and the genal region (normally one in the Ditrystia). In Hinton’s system, all the long tactile setae of Hepialidae are regarded as homologous with the Ditrystia and V1 therefore is assumed missing and a new seta, G2, considered present.



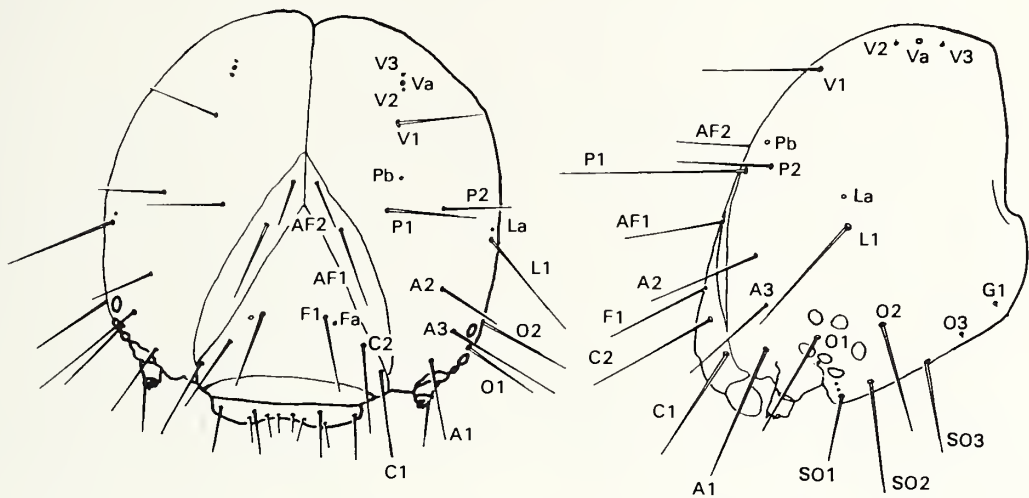
Figs. 23–26. Scanning electron micrographs. 23. Prothoracic (TI) claw of *Korscheltellus gracilis*, 1,315 \times . 24. Prothoracic (TI) claw of *Sthenopsis auratus*, 920 \times . 25. Abdominal proleg of *Sthenopsis auratus*, 820 \times , arrow on outer crochet. 26. Abdominal proleg of *Korscheltellus gracilis*, 1,455 \times , arrow on outer crochet.

Since *Yponomeuta* exhibits Ditrysiian chaetotaxy except for the presence of only two micro-vertex setae, the macro seta anterior to V2 is necessarily V1. This arrangement of micro and macro setae is identical to the Hepialidae and, therefore, the hepialid macro seta P2 of Hinton (1946) is regarded as V1 (compare Figs. 27 and 28). Hasenfuss (1969) suggests that the resulting rearrangement supports the view that Hinton's micro seta G2 is actually homologous with O3, with the result that the chaetotaxy of the Hepialidae is identical to that of the Ditrysia.

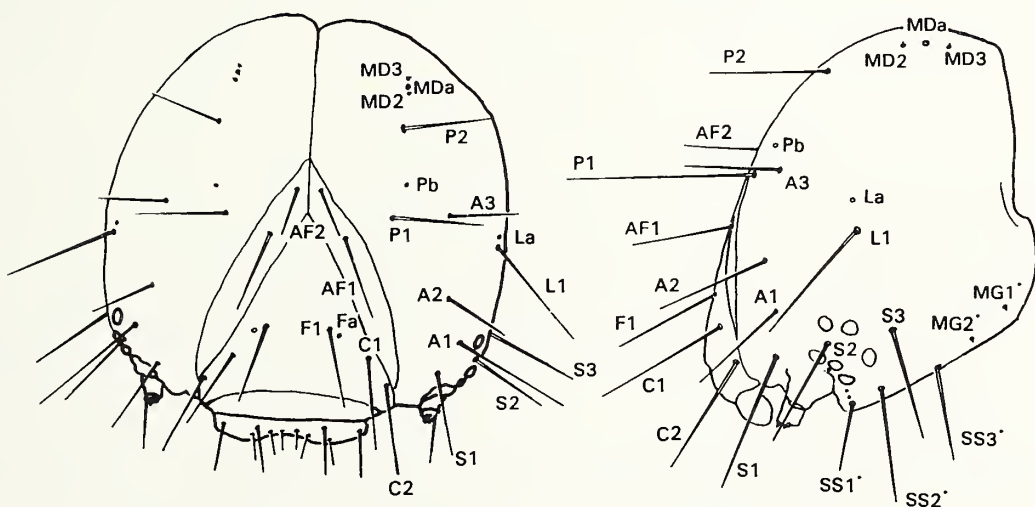
Stehr (1987) produced a system adopted by Wagner (1987) (Fig. 29) modifying Hinton's (1946) homology and terminology of the head. The major concern was that the micro-vertex setae (V series) and genal seta (G series) were proprioceptors homologous with the rest of the body and should be renamed in accordance with Hinton's system as microdorsal (MD) and microgenal setae (MG) (although to be consistent with Hinton's nomenclature, the genal setae should have been designated by MV). J. E. Rawlins (pers. comm.) suggests that while there may be some indications for homonymy of genal proprioceptors with the MV group on the thorax and abdomen, priority of usage favors retention of G and MV respectively as symbols for



27. Hinton (1946)



28. Hasenfuss (1969)



29. Wagner et al. (1989)

Figs. 27–29. Comparison of head chaetotaxy systems. Head of *Korscheltellus gracilis* re-drawn from Wagner et al. (1989). 27. Hinton (1946) system. 28. Hasenfuss (1969) system. 29. Wagner et al. (1989) system; SS and MG setae marked with * were not labeled in Wagner et al. (1989), Stehr (1987) system is used for these setae.

those groups. In Stehr (1987:290–291, 300) the designation of Hinton's **C1** and **C2** was accidentally reversed due to labeling error (F. W. Stehr, pers. comm.).

Nielsen and Kristensen (1989) adopted the nomenclature of Hasenfuss (1969) with the exception of the genal setae where they retain Hinton's (1946) **G2** instead of **O3** as used by Hasenfuss (1969). Kristensen (1984), in a discussion of the ground plan of the lepidopteran larval head, stated the retention of **G2** instead of **O3** "seems most natural from a phylogenetic point of view," because the genal position of the seta is ancestral in the Lepidoptera (N. P. Kristensen, pers. comm.). We have retained **O3** in this paper pending future reevaluation of cranial chaetotaxy.

The contrast between the classifications of Hinton (1946) and Hasenfuss (1969) can be represented cladistically for the **P** and **V** setae. In a cladistic representation, setae are terminals and homologies are nodes. The use of branching diagrams has no necessary implication for the ultimate origins of these morphological features although one might attempt to explore the implications with respect to ontogeny or phylogeny (Nelson, 1989).

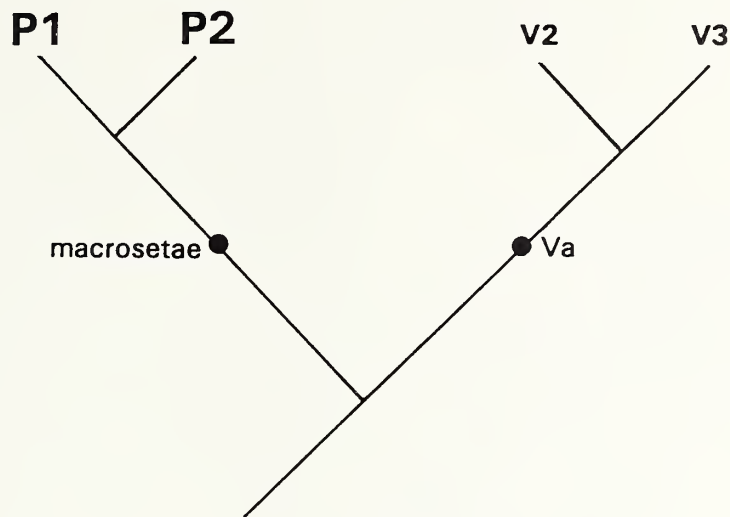
The classification of seta **P2** is inferred by Hinton (1946) to share closer relationship to the macroseta **P1** than to microsetae **V2/V3** (Fig. 30). The principles by which homologies are recognized for different setal groups were not explicitly stated by Hinton or Hasenfuss, although Hasenfuss (1963) supported a cladistic approach to phylogenetic classification in general. Hasenfuss (1969) suggested that the relative distinction between "long" and "short" setae did not provide an adequate defining character for setal groupings in this context. The fact that **P2** is long was not sufficient to place it only with **P1** because the "long" character would also place it within several other setal groups. Hasenfuss argued that the position of pore **Va** provides a defining character identifying a sister group relationship between **V3** and **V2** (i.e., the setae share a closer relationship to each other than with any other setae). To this group is added **V1** (formerly **P2**) by virtue of its position adjacent to and in line with **V2-V3** as also found in the Ditrystia (Fig. 31). With this reformulation of setal relationships, the setae of Hepialidae are not incongruent with respect to the Ditrystia and we support the nomenclature of Hasenfuss for the head capsule because the modifications are cladistically explicit and justifiable with reference to the Ditrystia. The status of **G2** also requires further clarification. The retention of **G2** by Nielsen and Kristensen (1989) while accepting **V1** of Hasenfuss requires the elimination of **O3**. We acknowledge that the present setal classifications are provisional pending future comprehensive evaluation of Lepidoptera larvae.

Thorax. Nielsen and Kristensen (1989) adopted Hardy's (1973) thoracic nomenclature, except for the **MD** and **MSD** microsetae where they used Hinton's system. Hardy (1973) applied a modified Hinton system but the **XD** pores on the prothorax (**TI**) were not labeled (Hardy, 1973:122, fig. 1). Hasenfuss (1963) reversed Hinton's subscripts for the **XD** pores so they were in linear order (a, b, c) and this order was adopted by Nielsen and Kristensen (1989). It is unclear why Hinton (1946) originally labeled these pores in the order b, a, c. He may have ordered the pores by their proximity to **XD1**. The pore labeled **XD_a** is closest to the **XD1** (Hinton, 1946:19, fig. 23). We use Hasenfuss's (1963) subscripts for the **XD** pores.

Wagner (1987) adopted Stehr's (1987) system of nomenclature (which is a modification of Hinton, 1946) for the prothorax (**TI**), but reversed the notation of **D2** and **SD2**. The identity of Hinton's **D2** as **SD2** presents a further example of prob-

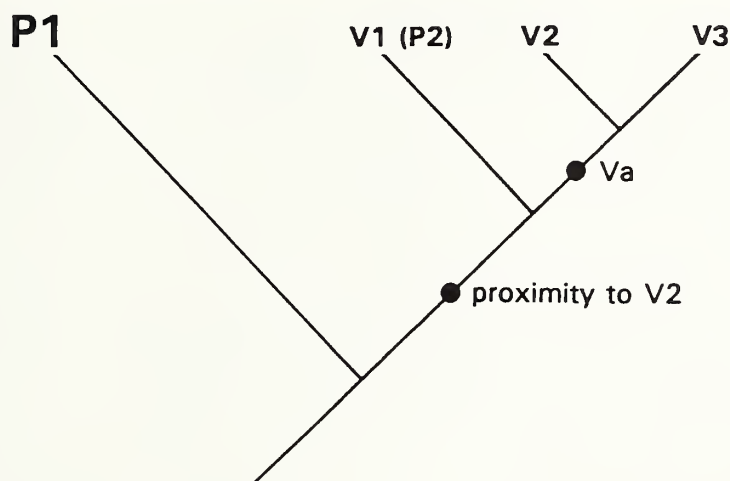
30

Hinton (1946)



31

Hausenfuss (1969)



Figs. 30–31. Cladistic representation of the vertex setae using (30) Hinton (1946) and (31) Hausenfuss (1969). Hinton's classification treats setal size as an informative character for **P1** and **P2**. This classification is altered by Hausenfuss to include Hinton's "P2" as part of the vertex group with the informative character being its proximity to **V2/V3**.

lematical setal relationships. Nielsen and Kristensen (1989) acknowledged Wagner's (1987) notation, but retained Hinton's usage pending further explanation of the rationale. Wagner (1987) noted that the designated **SD** setae are thin in comparison to **D2** (**SD2** of Hinton, 1946). Based on first instars, the two pronotal setae most similar in length and socket size are what Wagner (1987) calls **SD1** and **SD2** (**D2** of Hinton) (Figs. 19, 21). However, unlike post-first instars, setae **SD1** and **SD2** are thicker, longer and insert into larger sockets than **D2**.

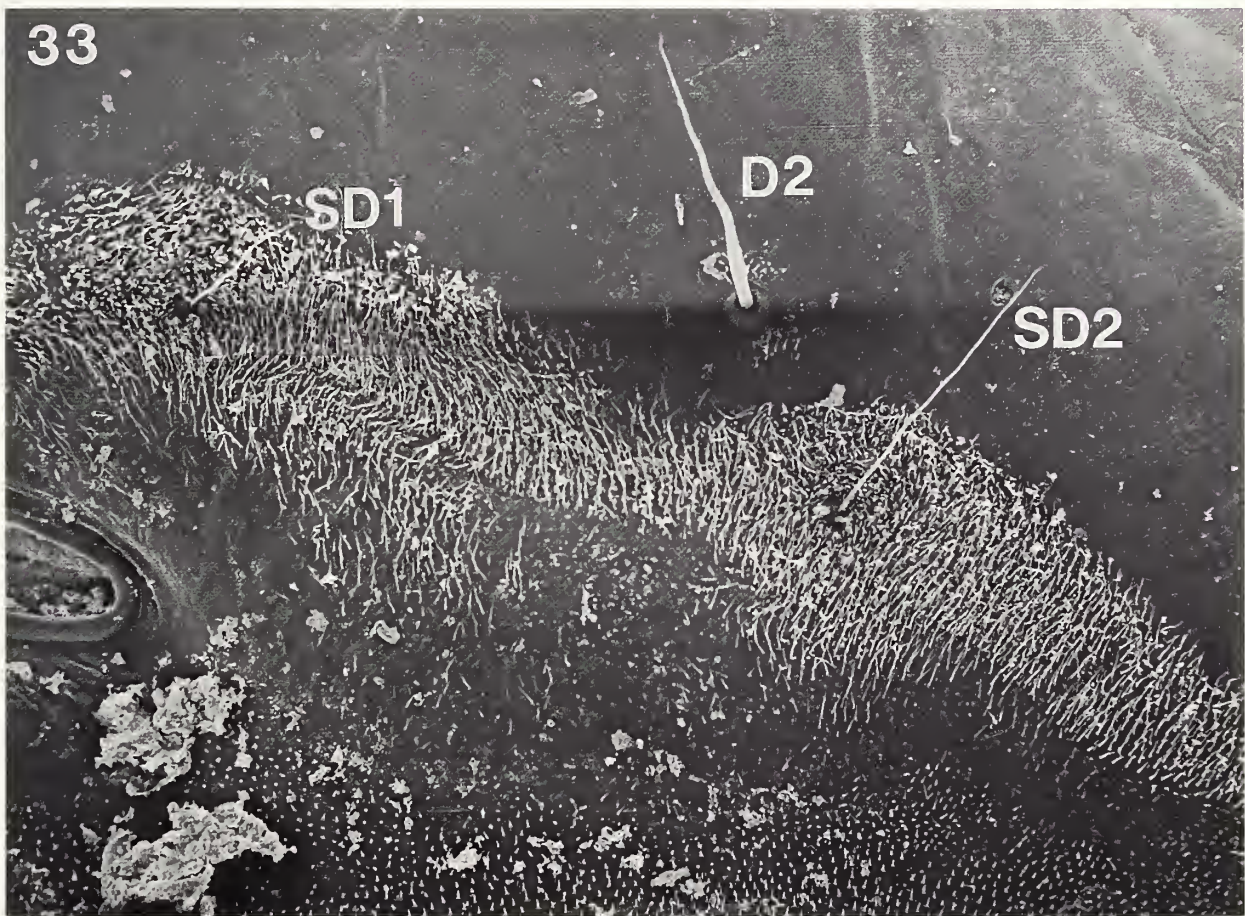
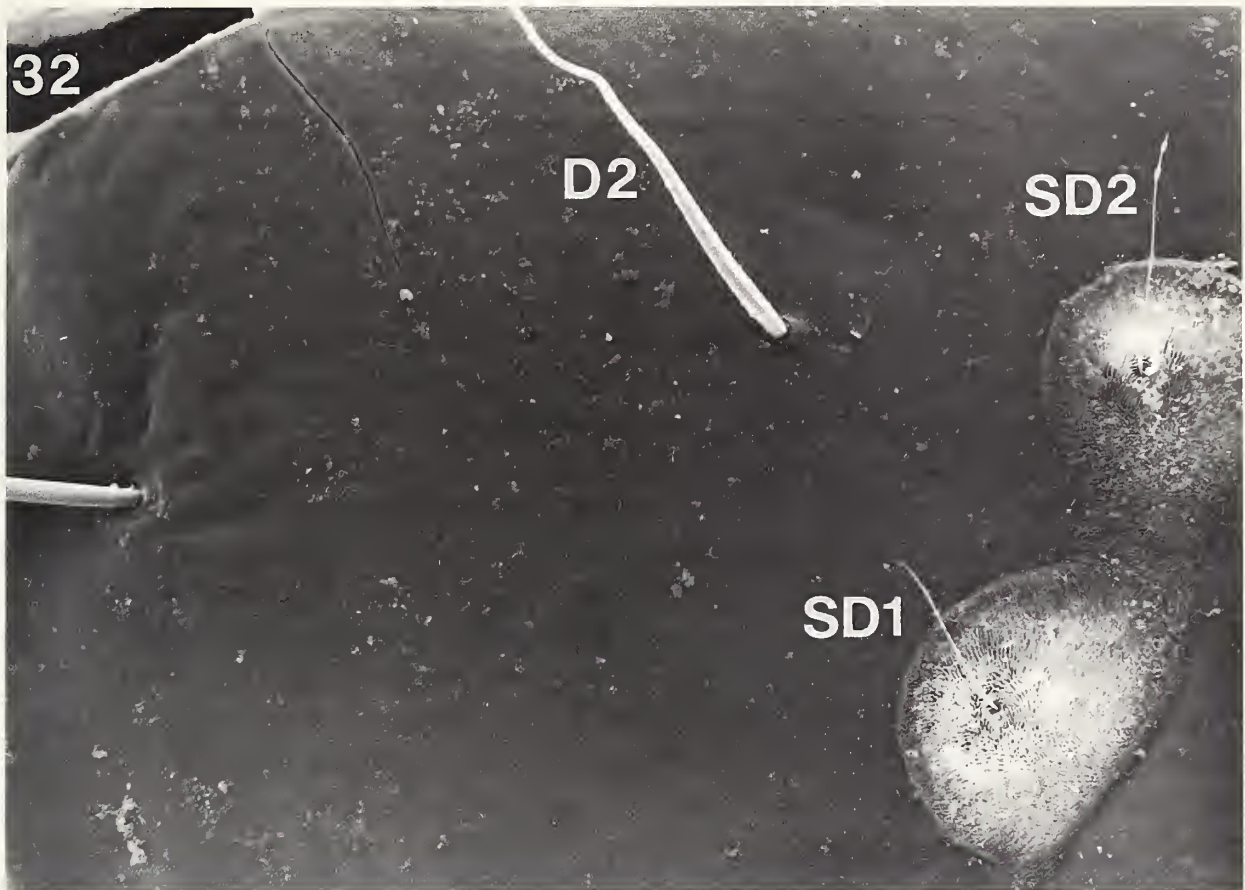
The **SD** setae (sensu Wagner, 1987) are subtended by dense microtrichia in later

instars of *K. gracilis* and *S. auratus*, as in some other Hepialidae (e.g., Fig. 32) (see also Martyn, 1960; Elder, 1978; Grehan, 1981; Nielsen and Kristensen, 1989). In still other hepialid species the seta **D2** (sensu Wagner, 1987) shares a microtrichial bed with both **SD** setae, but never with only one of them. The **SD** association with microtrichia may represent an exoporian trait as it is also present in the hepialoid sister group Mnesarchaeidae (Fig. 33) but not outside the Exoporia. Nielsen and Kristensen (1989:94) suggest that the presence of all three setae within a single "melanized depression" (=microtrichial bed of this paper) is an apomorphy for the Hepialidae sensu lato. First instar *K. gracilis* and *S. auratus* have no microtrichial bed associated with the **SD** setae or **D2** (also the case for other first instar Hepialidae), but they share a thinly melanized section of the shield. The setal size and presence of microtrichia surrounding the **SD** setae vary, but the setae consistently share homologies that exclude **D2** in all species reported and we therefore support Wagner's (1987) revision of nomenclature.

Abdomen. Hinton's (1946) system of abdominal nomenclature has not received modification in the literature, but requires critical examination comparable to that applied to the head capsule by Hasenfuss (1969). In particular are problems of serial homology or homonymy of the thoracic and abdominal **L** setae (D. L. Wagner, pers. comm.). Mutuura (1980) has suggested abdominal musculature as one source of characters for comparing pinacula/setal homologies between abdominal segments.

PHYLOGENY AND HEPIALID CHAETOTAXY

Chaetotaxy has historically provided useful phylogenetic characters, but the alternative nomenclatural choices currently available for hepialids represent a significant problem for recognizing setal homologies. Setal and pore characters currently recognized by all workers as "characteristic" for larvae of Hepialidae are based on Gerasimov (1937, 1952) and Hinton (1946) and include the following: The frons pore (**Fa**) is laterad and slightly ventral to **F1** seta. The Adfrontal pore (**Afa**), anterior pore (**Aa**), posterior pores (**Pa**, **Pb**), ocellar (stemmatal) pores (**Oa**, **Ob**) and genal pore (**Ga**) are absent. Setae **A3**, **A2**, and **P2** (of Hasenfuss, 1969) are almost in line running between the stemmata and **V1**, with **P2** caudad of **P1**. Two microsetae are present in the genal region: **O3** (of Hasenfuss, 1969) and **G1**. Stemmata (ocelli) are arranged in two vertical columns. The prothoracic shield includes **L1**, **L2** and sometimes **L3** in post-first instars. The prothorax has two subventral setae (**SV1** and **SV2**) and two midventral setae (**MV2** and **MV3**). Prothoracic setae **SD1** and **SD2** (of Wagner, 1987) are diagonally positioned and thin in comparison to **D2** in post-first instars. Seta **MV3** is elongate on **T1** in post-first instar larvae. The mesothorax (**TII**) has **MD1**, **MSD1** and **MSD2** on the same pinacula anterad of **SD1** and **SD2**. Seta **MD1** is often elongate in comparison with the **MSD** setae. There is only one subventral seta (**SV1**) on **TII** and **TIII**; there are two (**SV1** and **SV2**) on the prothorax. On the abdomen, setae **SD1** and **SD2** are on the same pinacula with **SD2** shorter and thinner than **SD1**. Setae **L1** and **L2** are near the spiracle with **L1** being farthest caudad and **L2** being closer and ventrad of the spiracle (**L2** is incorrectly described as being caudad of **L1** and spiracle, and **L1** ventrocaudad to spiracle in Wagner [1987]). On post-first instars, **L3** is anterad and ventrad of the spiracle on segments **A1**–**A8**. On segments **A2**–**A7**, **MV3** is elongate and grouped with the **SV** setae. Wagner (1987) identified additional hepialid larval characters: **Head**: Seta **O3** (of Hasenfuss,



Figs. 32–33. Scanning electron micrographs. 32. SD and D2 setae of *Trioxycanus* sp. showing the microtrichial bed shared by the SD setae, 65 \times . 33. SD and D2 setae of *Mnesarchaea* sp. showing the microtrichial bed shared by the SD setae, 80 \times .

1969) is approximately half-way between **G1** and **SO3**. **Prothorax: SD1** and **SD2** are diagonally positioned in a darkened pinacula. In some species **SD** pinacula encompassing **D2** in a darkened pigmented area with dense microtrichia.

Nielsen and Kristensen (1989) commented on several characters that appear to represent exoporian or hepialid apomorphies, but are also represented in other Lepidoptera. They suggest the presence of **MXD1** to be a glossatan groundplan character, and its absence an Exoporian groundplan trait (but not a synapomorphy since this proprioceptor is found in some but not all Eriocraniidae). Wagner (1987) identified the presence of two microgenal setae on the head as unique characteristics of Hepialidae, but this does not apply using the classification of Hasenfuss. Adult Hepialidae provide only one recognized synapomorphy (absence of tibial spurs) and this is not a universal character for the Hepialidae sensu lato (Viette, 1949; Wagner and Tindale, 1988; Nielsen and Kristensen, 1989:113). The cladistic status of many chaetotactic characters recognized for the Hepialidae require clarification. A cladistic classification of setae, as proposed in this paper for the **V** series, provides a measure of confidence for comparative chaetotaxy and may help determine which setal characters qualify as hepialid synapomorphies. Complementary to this kind of evaluation is the inclusion of a greater range of larval records, including first instars which are extremely easy to obtain from fertilized eggs.

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LITERATURE CITED

- Aitkenhead, P. and C. R. B. Baker. 1964. The larvae of the British Hepialidae. *Entomologist* 97:25-38.
- Birket-Smith, S. J. R. 1984. Prolegs, legs, and wings of insects. *Entomonograph* 5:1-128.
- Bonan, G. B. and H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. *Annu. Rev. Ecol. Syst.* 20:1-28.
- Boudinot, J. 1991. *Biologie d'Aenetus cohici* Viette (Lepidoptera: Hepialidae). In: J. Chazeau and S. Tillier (eds.), *Zoologia Neocaledonica*, Vol. 2. *Mem. Mus. natn. Hist. nat., (A)*, 149:167-175. Paris.
- Common, I. F. B. 1990. *Moths of Australia*. E. J. Brill, New York.
- Dyar, H. G. 1895. The classification of the Lepidoptera on larval characters. *Am. Nat.* 29: 1066-1072.
- Elder, R. J. 1978. Notes on the biology and descriptions of the life stages of *Oncopera parva* Tindale (Lepidoptera: Hepialidae). *J. Aust. Entomol. Soc.* 17:5-11.
- Forbes, W. T. M. 1923. The Lepidoptera of New York and neighboring states. *Cornell Univ. Agr. Exp. Sta. Mem.* 68:1-729.
- Fracker, S. B. 1915. The classification of lepidopterous larvae. III. *Biol. Monogr.* 2:1-169.
- Gerasimov, A. M. 1935. Zur Frage der Homodyamie der Borsten von Schmetterlingsraupen. *Zool. Anz.* 112:117-194.

- Gerasimov, A. M. 1937. Hepialidenraupen (Lepid.). Ent. Zeit. 51:81–84.
- Gerasimov, A. M. 1952. Lepidoptera, Part 1. Caterpillars. Zool. Inst. Acad. Nauk USSR. New Ser. No. 56, Fauna USSR. Insects-Lepidoptera. 2:1–338.
- Grehan, J. R. 1981. Morphological changes in the three-phase development of *Aenetus virescens* larvae (Lepidoptera: Hepialidae). New Zealand J. Zool. 8:505–514.
- Grehan, J. R., A. Moeed and M. J. Meads. 1983. Observations on *Trioxycanus enysii* (Butler) (*sensu* Meyrick, 1890) (Lepidoptera: Hepialidae) on Kapiti Island, New Zealand, with a description of larval chaetotaxy. New Zealand Entomol. 7:408–413.
- Grehan, J. R., B. L. Parker, D. L. Wagner, J. Rosovsky and J. Aleong. 1992. Root damage by the conifer swift moth: a mortality factor in montane red spruce regeneration. For. Sci. (in press).
- Hain, F. P. 1987. Interactions of insects, trees, and air pollutants. Tree Phys. 3:93–102.
- Hardy, R. J. 1973. Larval chaetotaxy of thorax and abdomen of *Fraus simulans* Walker (Lepidoptera: Hepialidae). J. Aust. Entomol. Soc. 12:121–123.
- Hasenfuss, I. 1963. Eine vergleichend-morphologische Analyse der regulären Borstenmuster der Lepidopterenlarven. Studien zur Methodik der vergleichenden Morphologie der Borstenmuster und zur phylogenetischen Deutung der Abwandlungen der regulären Borstenmuster der Lepidopterenlarven. Zeit. Morph. Okol. Tiere 52:197–364.
- Hasenfuss, I. 1969. Zur Homologie der Borstenmusterelemente der Larven-Kopfkapsel einiger monotrýsischer Lepidoptera. Beitr. Ent. 19:289–301.
- Heinrich, C. 1916. On the taxonomic value of some larval characters in the Lepidoptera. Proc. Entomol. Soc. Wash. 18:154–164.
- Hinton, H. E. 1946. On the homology and nomenclature of setate of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. Trans. Roy Entomol. Soc. Lond. 97:1–37.
- Hornbeck, J. W. and R. B. Smith. 1985. Documentation of red spruce growth decline. Can. J. For. Res. 15:1199–1201.
- Klein, R. and T. D. Perkins. 1988. Primary and secondary causes and consequences of contemporary forest decline. Bot. Rev. 54:2–24.
- Kristensen, N. P. 1978. A new family of Hepialoidea from South America, with remarks on the phylogeny of the suborder Exoporia (Lepidoptera). Entomol. Germ. 4:272–294.
- Kristensen, N. P. 1984. The larval head of *Agathiphaga* (Lepidoptera, Agathiphagidae) and the lepidopteran ground plan. Syst. Entomol. 9:63–81.
- Leonard, J. G., D. R. Tobi and B. L. Parker. 1991. Spatial and temporal distribution of *Korscheltellus gracilis* larvae (Lepidoptera: Hepialidae) in the Green Mountains, Vermont. Environ. Entomol. 20:371–376.
- Martyn, E. J. 1960. The ecology of *Oncopera intricata* Walker and *Oncopera rufobrunnea* Tindale (Lepidoptera, Hepialidae) with notes on the classification of the genus *Oncopera* in relation to larval taxonomy. Tasmanian Depart. of Agric. Res. Bull. 3.
- McCabe, T. L. and D. L. Wagner. 1989. The biology of *Sthenopis auratus* (Grote) (Lepidoptera: Hepialidae). J. New York Entomol. Soc. 97:1–10.
- Mutuura, A. 1980. Morphological relations of sclerotized and pigmented areas of lepidopterous larvae to muscle attachments, with applications to larval taxonomy. Can. Entomol. 112:697–724.
- Nelson, G. 1989. Cladistics and evolutionary models. Cladistics 5:275–289.
- Nielsen, E. S. 1989. Phylogeny of major Lepidopteran groups, pp. 281–294. In: B. Fernholm, K. Bremer and H. Jörnvall (eds.), The Hierarchy of Life. Elsevier Science Publishers, Amsterdam.
- Nielsen, E. S. and N. P. Kristensen. 1989. Primitive Ghost Moths, morphology and taxonomy of the Australian genus *Fraus* Walker (Lepidoptera: Hepialidae s. lat.). Monographs on Australian Lepidoptera, Vol. 1. CSIRO.
- Packard, A. S. 1895. On the larvae of the Hepialidae. J. New York Entomol. Soc. 3:69–73.

- Pitelka, L. F. and D. J. Raynal. 1989. Forest decline and acidic deposition. *Ecology* 70:2–10.
- Reiners, W. A. and G. E. Lang. 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. *Ecology* 60:403–417.
- SAS Institute. 1985. *SAS User's Guide: Basics, Version 5 Ed.* SAS Institute, Cary, N.C.
- Siccama, T. G., M. Bliss and H. W. Vogelmann. 1982. Decline of Red Spruce in the Green Mountains of Vermont. *Bull. Torrey Bot. Club* 109:162–168.
- Silver, W. L., T. G. Siccama, C. Johnson and A. H. Johnson. 1991. Changes in red spruce populations in montane forests of the Appalachians 1982–1987. *Am. Mid. Nat.* 125: 340–347.
- Smith, W. H. 1991. Air pollution and forest damage. *Chem. Engin. News* 69:30–43.
- Stehr, F. W. 1987. Order Lepidoptera. Pages 288–305 *in*: F. Stehr (ed.), *Immature Insects*. Kendall-Hunt, Dubuque, Iowa.
- Tobi, D. R., W. E. Wallner and B. L. Parker. 1989. The conifer swift moth, *Hepialus gracilis*, and spruce-fir decline. Pages 361–363 *in*: *Proceedings of the US-FGR Symposium: Effects of Atmospheric Pollutants on the Spruce-Fir Forests of the Eastern United States and Federal Republic of Germany*. USDA Forest Service, Northeastern For. Exp. Sta. Gen. Tech. Rep. Broomall, PA.
- Tobi, D. R., J. G. Leonard, B. L. Parker and W. E. Wallner. 1992. Survey methods, distribution, and seasonality of *Korscheltellus gracilis* (Lepidoptera: Hepialidae) in the Green Mountains, Vermont. *Environ. Entomol.* 21:(in press).
- Viette, P. 1949. Contribution a l'étude des Hepialidae (12^e note). *Genres et synonymie*. *Lambillionea* 1949:101–104.
- Vogelmann, H. W., T. D. Perkins, G. J. Badger and R. M. Klein. 1988. A 21-year record of forest decline on Camels Hump, VT USA. *Eur. J. For. Pathol.* 18:240–249.
- Wagner, D. L. 1987. Hepialidae. Pages 347–349 *in*: F. Stehr (ed.), *Immature Insects*. Kendall-Hunt, Dubuque, Iowa.
- Wagner, D. L. 1988. Taxonomic status of *Korscheltellus* Börner in North America (Lepidoptera: Hepialidae). *J. New York Entomol. Soc.* 96:345–354.
- Wagner, D. L. and N. B. Tindale. 1988. An appraisal of *Gazoryctra* Hubner (Hepialidae) and description of a new species from Arizona and New Mexico. *J. Lepidopterists' Soc.* 43: 204–212.
- Wagner, D. L., D. R. Tobi, B. L. Parker, W. E. Wallner and J. G. Leonard. 1989. Immature stages and natural enemies of *Korscheltellus gracilis* (Lepidoptera: Hepialidae). *Ann. Entomol. Soc. Am.* 82:717–724.
- Wagner, D. L., D. R. Tobi, W. E. Wallner and B. L. Parker. 1991. *Korscheltellus gracilis* (Grote): a pest of red spruce and balsam fir roots (Lepidoptera: Hepialidae). *Can. Entomol.* 123:255–263.
- Yasuda, T. and K. Abe. 1986. *Endoclita hosei* Tindale (Lepidoptera: Hepialidae) attacking *Eucalyptus* in Sabah, with descriptions of the immature and imaginal stages. *Appl. Entomol. Zool. Tokyo* 21:417–423.

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